Pivotal temperatures for loggerhead turtles (*Caretta caretta*) from northern and southern nesting beaches

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The pivotal incubation temperature (that giving 50% of each sex) was estimated for two clutches of eggs from loggerhead sea turtles (*Caretta caretta*) nesting in each of three areas along the east coast of the United States: North Carolina, Georgia, and southern Florida. All pivotal temperatures were close to 29.0°C. There was a significant difference between the pivotal temperatures of the two clutches from Florida. As an index of beach temperature, data on incubation durations in the three areas were collated and analysed: even during the warmest part of the season, incubation took about 6 days longer in North Carolina than in Georgia, and about 10–14 days longer than in Florida. Since there was no evidence that pivotal temperatures in North Carolina were lower than those of turtles nesting further south, it is likely that a higher percentage of males are produced on the North Carolina beaches, but data on pivotal temperatures of additional clutches are needed before this prediction can be made with confidence. The possible use of incubation duration for estimating sex ratios of hatchlings is discussed.

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La température d'incubation de pivotement (celle qui produit 50% de chaque sexe) a été estimée chez des Tortues de mer *Caretta caretta* le long de la côte est des États-Unis; deux masses d'oeufs ont été étudiées en chacune de trois régions, Caroline du Nord, Géorgie et sud de la Floride. Toutes les températures de pivotement se situent autour de 29,0°C. Il y avait une différence significative entre les températures de pivotement des deux masses d'oeufs de la Floride. Afin de déterminer un indice de température de la plage, des données sur la durée de l'incubation dans les trois régions ont été compilées et analysées : même au cours de la partie la plus chaude de la saison, l'incubation en Caroline du Nord a duré 6 jours de plus qu'en Géorgie et environ 10–14 jours de plus qu'en Floride. La température de pivotement des tortues de Caroline ne semble pas plus basse que celle des tortues plus australes; il est donc permis de croire que les masses d'oeufs de Caroline produisent un pourcentage plus élevé de mâles, mais cette affirmation ne pourra être avancée avec certitude qu'après obtention de données sur les températures de pivotement d'autres masses d'oeufs. La possibilité d'estimer le rapport mâles : femelles d'apres la durée de la période d'incubation fait l'objet d'une discussion.

[Traduit par la revue]

Introduction

The direction of sexual differentiation in a variety of reptiles depends on the temperatures during incubation of the eggs. In turtles, higher temperatures result in female phenotypes, lower temperatures in male phenotypes. The temperature in between, giving 50% of each sex, is called the pivotal temperature (Mrosovsky and Yntema 1980), the threshold temperature (Bull 1980), or the critical temperature (Pieau 1976). The more vivid term pivotal is preferred because threshold is widely used in other contexts, and because critical is already used for the critical period within incubation, approximately the middle third in turtles, when temperature effects are important.

An interesting question arises about the pivotal temperatures of species that breed over a range that includes thermally different nesting areas. Is the pivotal temperature different for different populations (Bull 1980; Mrosovsky 1980)? Or, if the pivotal temperature remains the same, is the same sex ratio produced in different parts of the breeding range (Bull et al. 1982a)? Another possibility, especially for sea turtles with their freedom to travel widely and intermix, is that there are male- and female-producing regions within the range.

Previous data are summarized in Table 1. For painted turtles (*Chrysemys picta*) there is a tendency for lower pivotal temperatures to occur in more northern populations. However, given the sensitivity of sexual differentiation to small changes in temperature, caution is appropriate in comparisons between experiments by different investigators using different procedures. In the one comparison in which the same investigators compared two populations, the southern

(Tennessee) turtles had a lower pivotal temperature than the northern (Wisconsin) ones.

Another complication with the freshwater species shown in Table 1 is that they have two pivotal temperatures, that is, females are produced at both warm and cool temperatures, with the intermediate range resulting in males. This means that equal sex ratios might be produced in cooler and warmer parts of the range in various ways. In northern populations the upper pivotal temperatures might be lower or the lower pivotal temperatures might be higher, or both. The latter seems to be the case with the Ontario snapping turtles (*Chelydra serpentina*; Table 1).

With loggerhead turtles (*Caretta caretta*) there appears to be only one pivotal temperature. This makes predictions straightforward: if adjustments of pivotal temperature are the means for producing equal numbers of each sex in thermally different parts of the range, then in cooler areas of the range the pivotal temperature must be lowered to maintain the proportion of females. However, for loggerhead turtles nesting in Australia, it was the eggs from Mon Repos, a black sand beach with higher temperatures than the white coral sands of Heron Island, that had the lower pivotal temperature. Both the values were lower by 1.3°C or more than the pivotal temperature for Georgia, U.S.A.

There are several reasons why these apparent differences cannot be accepted with confidence. In the work on eggs from Georgia, only 2°C intervals were used. The experiment provided the first clear evidence that sexual differentiation in sea turtles depends on incubation temperature, but was not designed to give a precise pivotal temperature (Yntema and

TABLE 1. Approximate pivotal temperatures of turtles: comparisons between eggs from different parts of the range (data are from experiments in which eggs were incubated at various constant temperatures)

	Pivotal temperatures[a] (°C)		Reference
Chrysemys picta (painted turtle)			
Ontario	20.0	27.5	Schwarzkopf and Brooks 1985
Wisconsin	?	29.0	Bull et al. 1982a
Nebraska	22.5	?	Gutzke and Paukstis 1984
Tennessee	?	<28.0	Bull et al. 1982a
Graptemys pseudogeographica (map turtle)[b]			
Wisconsin		29.4	Bull et al. 1982a
Tennessee		29.0	Bull et al. 1982a
Chelydra serpentina (snapping turtle)			
Ontario	23.0	27.0	Brooks and Nancekivell 1984
New York	21.0	29.0	Yntema 1976
Caretta caretta (loggerhead turtle)			
Georgia		30.0	Yntema and Mrosovsky 1982
Heron Island, Queensland, Australia		28.7	Limpus et al. 1985
Mon Repos, Queensland, Australia		27.7	Limpus et al. 1985

[a]Some species have a single pivotal temperature; in other species there is an upper and a lower pivotal temperature.
[b]Not known if this species has more than one pivotal temperature.

Mrosovsky 1982). Another problem is that the methods for the experiments in America and Australia differed. In the former, eggs were incubated singly, in the latter, in groups of 10; this might have influenced the dispersal of metabolic heat or evaporative cooling. In the results from Australia, the curve relating sex ratio to temperature was flatter than that for the North American data; both sexes were produced over a wider range of temperatures. Probably this resulted from the greater temperature variation in the Australian work. Standard deviation of the mean temperature within the incubators was up to ±0.5°C; the range of temperature must therefore have been greater. For the sample from Georgia the range was ±0.5°C. In both these experiments, temperature values were taken from thermometers approximately at the centre of the incubators; variation between shelves was not described and may well have differed.

Methods of data analysis also differed. In our work the temperature giving 50% of each sex was taken as the pivotal temperature (Yntema and Mrosovsky 1980, 1982). This was usually obtained by interpolation between the two sex ratios on either side of 50% (Mrosovsky et al. 1984). Limpus et al. (1983, 1985) took all values into account and fitted a curve, from which they read the 50% value. It is debatable whether their method is appropriate. If each sex is being produced at temperatures 2°C or so above or below the pivotal level as a result of some temperature variations within the incubators set at those values, then it would not be appropriate to take those data into account. For instance, 28.7°C is given as the 50% point for the Heron Island clutches but at 29.0°C only 45% of the turtles sexed were female. A 50% value would therefore occur somewhere above 29.0°C, but because there were some females being produced at temperatures as low as 26°C the curve-fitting method gave a value below 29.0°C (Limpus et al. 1985). Some of these points do not apply to the comparisons between the two areas within Queensland, for which the same methods were used. However, in the one comparison in which the eggs were set in the same container, no significant difference between the areas was found.

These considerations illustrate some of the difficulties in comparing pivotal temperatures between different populations of turtles. The fundamental problem is that small differences in temperature make a considerable difference to sex ratio and many factors make a small difference to temperature. Among these are the position of the egg in the incubator, type of substrate, moisture and evaporative cooling, methods of measuring temperature, and accuracy of calibration of thermometers.

The present experiments were undertaken in an attempt to reduce some of these complications. Loggerhead turtle eggs were collected from three beaches in the southeastern United States, from North Carolina to southern Florida. They were incubated in Toronto at several constant temperatures close to the approximate pivotal temperature obtained previously (Yntema and Mrosovsky 1982). Care was taken to standardize and specify the incubation methods as much as possible. In addition, we obtained and collated data on incubation durations in the field; these provided an indirect index of temperature.

Methods

Source of eggs

The locations of the three collecting areas are shown in Fig. 1. Collecting dates and information on the mother turtles are provided in Table 2, just in case these turn out to be important variables.

Transport

The eggs were taken from the nests and placed in Styrofoam carrying boxes. They were accompanied in person on the journey to Toronto to ensure that they were not put through X-ray machines or handled roughly; turtle eggs should not be subjected to mechanical disturbance (Limpus et al. 1979). All clutches were in the incubators at Toronto within 17–25 h of being laid. By that time the eggs had still not started to spot (formation of white spot on the shell near the top of the egg indicating attachment of the membrane to the shell).

Incubation methods

Eggs were incubated singly in 600-mL plastic containers according to method 2 of McLean et al. (1983), with minor modifications (Fig. 2). Each container was covered by an inverted transparent plastic petri dish (14 cm diam., 1.5-cm lip); this made it easy both to see the eggs and to remove the lid without disturbing them. At the top of
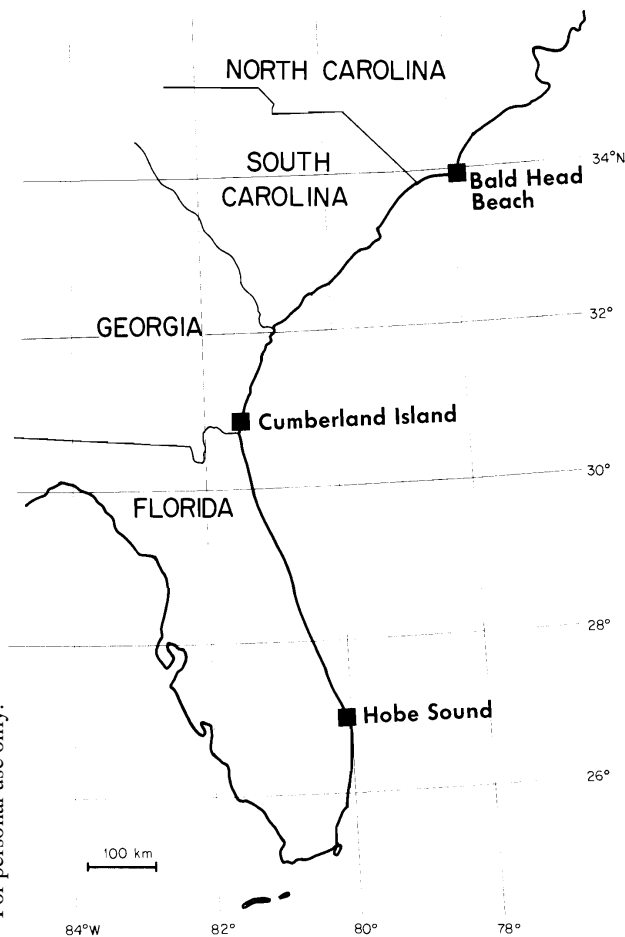
FIG. 1. Map showing the locations of the beaches from which the eggs were taken.

FIG. 2. Scale drawing of containers used for incubating turtle eggs individually (see text for further details).

each container eight holes (2.5 mm diam.) were punched around the circumference to standardize air flow. At the start of incubation, 65 ± 10 mL of water was added to moisten the foam sponge base. After the egg was in place on the sponge, it was surrounded by wet vermiculite. Only dechlorinated water was used.

The egg containers were set in Precision Scientific incubators adjusted to run at temperatures bracketing the expected pivotal level.

Temperature measurements and correction factor

Sybron/Taylor mercury thermometers with certified calibration against platinum resistance thermometers, calibrated by the U.S. National Bureau of Standards, were used to check or recalibrate all thermometers used in these experiments. Mercury thermometers, with 0.1°C graduations, were placed approximately at the centre of the various shelves in the incubators; these thermometers were surrounded with glycerine and readings were taken with alacrity when the incubator doors were opened. Temperatures were read about once a day. Although the incubator temperatures were not continuously monitored, inexpensive maximum–minimum thermometers, which could not be accurately calibrated in absolute terms, gave assurance that no important fluctuations had occurred between daily temperature readings. In 1984 fewer thermometers were available and each incubator shelf did not have a thermometer every day; however, subsequent checks showed that the thermal differences among shelves were similar in 1984 to those in subsequent years.

Because of the moisture in the egg containers, it was expected that the [eggs themselves would] be cooler than the air in the centre of the
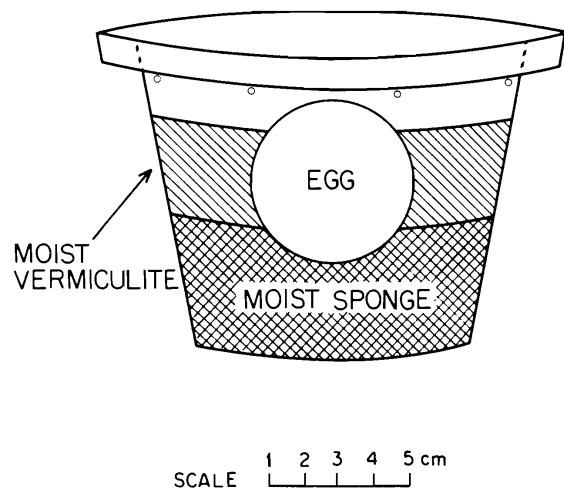
shelves. To assess this, a Yellow Springs Instruments 402 telethermometer probe was inserted through a small hole in the container lid and then into an egg. The probe had been previously calibrated against the standard. After allowing many hours for thermal equilibrium to be reached, it was found that the egg temperature was 0.5°C below that of the standard mercury thermometer placed nearby. Therefore a −0.5°C correction factor for evaporative cooling was applied to all temperatures taken in the incubators. This is similar to the −0.3°C correction determined previously; slightly different container lids and substrates were used in those experiments (Mrosovsky et al. 1984).

Moistening and humidity

Uncovered bowls of water were set at the bottom of the incubators. On day 16 or 17 and day 38, 65 ± 10 mL of water was added from these bowls to each egg container. Humidity within the containers was high: beads of moisture were often visible on the transparent covers or on the eggs themselves. At hatching, water was nearly always still present around the base of the sponge. In 1986, humidity was measured with a Vaisala Humicap meter with an HMP 14 probe. Humidity was always >88% and usually >90% when measured; we could detect no major or reliable differences between incubators. Probably humidity was higher than the values given, and may well have been close to 100% but this could not be verified because when the probe was inserted into a container the air mass around the egg was disturbed. Allowing time for the air below the lid to resaturate with moisture also allowed time for the calibration of the probe to change.

Histology

Sex was determined from examination of sections of the gonads. Histological methods were those of Yntema and Mrosovsky (1980) with slight modifications given by Mrosovsky et al. (1984).

Hatching duration and miscellaneous information

The date of laying was taken as day 0. Hatching was considered to have occurred when the head and both front flippers protruded from the egg. One egg in the North Carolina 29.5°C incubator and one egg from the Florida 28.5°C incubator produced twins. One of the latter was dead and could not be sexed. Twins were counted as two animals for the sex ratio analysis and as one animal for the incubation durations.

Results

Hatch rates

Hatch rates for North Carolina, Georgia, and Florida

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TABLE 2. Source and details of eggs sampled

	Night laid and collected[a]	Clutch size	No. of eggs collected	Comments
Bald Head Beach, North Carolina (1984)				
Clutch A	10−11 July	117[b]	101	
Clutch B	10−11 July	59[b]	59	Turtle laying these eggs was small
Cumberland Island, Georgia (1985)				
Clutch C	15−16 July	118	80	Tag GA 6302, small turtle, 1st year seen nesting here, stringy filaments on the eggs
Clutch D	15−16 July	ca. 120	80	GA 7151, nested in previous seasons on Cumberland Island
Hobe Sound, Florida (1986)				
Clutch F	27−28 May	99[b]	80	Turtle laying these eggs was fairly small
Clutch G	27−28 May	150[b]	80	

[a]Second of the two dates was designated as day 1 of incubation.
[b]Doomed eggs: nest below the high-tide line.

samples were 95.6, 71.9, and 75.6%, respectively. The lower average hatch rate for Georgia was attributable to the clutch of eggs with stringy inclusions in their shells (53.8%). For the other clutch from this region the hatch rate was 90.0%.

It was possible to sex some of the turtles that did not hatch. The differences in sample sizes in Tables 3 and 4 enable the reader to determine from which temperature group these specimens came. The overall percentages of eggs producing turtles that could be sexed were 96.3, 79.4, and 90.0 for North Carolina, Georgia, and Florida, respectively. Differential mortality between the sexes cannot therefore be invoked to explain the temperature effects on sex ratio.

Constitution of temperature groups

The lowest shelves of the incubators used for the North Carolina sample (1984) had temperatures about 0.5°C below those at the centres of the incubators. Data for turtles from the lower shelves were therefore included with those for the next cooler incubators, or treated as a separate group if there was no cooler incubator within 0.5°C (Tables 3 and 4). The lowest shelves were not used in subsequent years.

For the Georgia sample, one incubator set at 29.3°C malfunctioned. After temperatures had fluctuated between 28.9 and 29.9°C, the eggs were transferred to two of the other incubators on day 18. Since the critical period for temperature effects on sexual differentiation in loggerhead turtles is roughly in the middle trimester of incubation (Yntema and Mrosovsky 1982), it was assumed that the experience in the initial incubator had little effect. Only the temperatures of the incubators containing the eggs after day 18 were taken into account.

The systematic changes in incubation duration as a function of different temperatures (Tables 4 and 6) suggests that reasonable assumptions were made about the transferred eggs and those on the lowest shelves. However, in case these decisions were unjustified in some way, a reduced data set is presented in Tables 5 and 6. These tables include only turtles from shelves that had held eggs in all 3 years. As the same three incubators were used and almost the same temperatures prevailed, 9.5°C range, the reduced data set pro-

vides a comparison involving fewer assumptions than the full data set.

Calculation of pivotal temperatures

The pivotal temperatures (Tables 3 and 5) were estimated by interpolation between points with sex ratios on either side of 50%; only points based on samples of more than 20 were used. If the sex ratio did not rise monotonically with temperature, two interpolations were made. For example, for North Carolina the percentage of females was slightly lower at 28.8 than at 28.5°C (Table 3). Sex ratios at both these temperatures were joined to the sex ratio at 29.5°C and two interpolated values for the pivotal temperature were obtained (29.0, 29.2°C). Both these interpolations are close to 29.2°C which actually produced 50% of each sex, but with a sample size of only eight.

Limits of accuracy in specification of temperatures

The fact that the percentages of females did not all invariably rise progressively between points that were only 0.5°C apart should not be surprising for several reasons. First, the ranges of the temperatures overlapped. Second, although it was clear from the maximum−minimum thermometers that fluctuations were slight, temperature was not monitored continuously. The values shown (Tables 3−6) may not correspond exactly to the mean temperatures. Third, the thermometers measured temperature in one place near the centre of shelves containing eggs. Differences in air currents or other factors might have caused slight differences between incubators for temperatures in other places. Despite these points, the experiment was more precise than previous ones in the specification of pivotal temperatures because the incubators were all set at values close to the pivotal; the temperatures were maintained sufficiently well to make comparisons between the clutches.

Geographic and clutch differences

There was no tendency for pivotal temperatures to become progressively lower in clutches collected further to the north. The overall pivotal temperatures for the Florida and North Carolina samples were very close to each other; at 29.0−29.2°C they were a little above those for the geographically intermediate Georgia sample (pivotal temperature just below

TABLE 3. Percent females produced for all turtles sexed for different incubation temperatures

	27.5 ±0.5°C	28.0 ±0.5°C	28.5 ±0.6°C	28.8 ±0.4°C	29.2 ±0.2°C	29.5 ±0.3°C	30.0 ±1.0°C	30.4 ±0.4°C	30.5 ±1.0°C	Estimated pivotal temp. (°C)
North Carolina	14.3 (7)[b]	10.3 (29)[c]	31.3 (32)[d]	20.8 (24)	50.0 (8)[e]	66.7[a] (24)	62.5 (8)[f]		100.0 (23)	29.0, 29.2
Georgia			66.7 (27)	65.7 (35)[h]		77.5[g] (40)[i]		100.0 (25)		Near but <28.5
Florida			26.5 (34)	35.3 (34)		64.9 (37)		92.3[g] (39)		29.2
Overall	14.3 (7)	10.3 (29)	39.8 (93)	43.0 (93)	50.0 (8)	70.3 (101)	62.5 (8)	95.3 (64)	100.0 (23)	29.0

NOTE: Sample sizes are given in parentheses. Range of incubation temperatures is indicated by ± values.
[a]Includes the twins, both females.
[b]Seven eggs from lowest shelf of 28.0°C incubator.
[c]Includes eight eggs from lowest shelf of 28.5°C incubator.
[d]Includes eight eggs from lowest shelf of 28.8°C incubator.
[e]Eight eggs from lowest shelf of 29.5°C incubator.
[f]Eight eggs from lowest shelf of 30.5°C incubator.
[g]One intersex not counted as female.
[h]Includes 10 eggs transferred from erratic incubator on day 18.
[i]Includes 15 eggs transferred from erratic incubator on day 18.

TABLE 4. Mean incubation durations in days for turtles that hatched for different incubation temperatures

	27.5 ±0.5°C	28.0 ±0.5°C	28.5 ±0.6°C	28.8 ±0.4°C	29.2 ±0.2°C	29.5 ±0.3°C	30.0 ±1.0°C	30.4 ±0.4°C	30.5 ±1.0°C
North Carolina	65.0 (7)[a]	60.9 (29)[b]	56.8 (32)[c]	54.8 (24)	53.3 (8)[d]	52.1 (22)	51.0 (8)[e]		48.8 (23)
Georgia			59.2 (26)	57.1 (30)[f]		55.0 (37)[g]		50.8 (22)	
Florida			58.8 (31)	56.6 (30)		53.3 (32)		50.3 (28)	
Overall	65.0 (7)	60.9 (29)	58.2 (89)	56.3 (84)	53.3 (8)	53.7 (91)	51.0 (8)	50.5 (50)	48.8 (23)

NOTE: Sample sizes are given in parentheses. Range of incubation temperatures is indicated by ± values.
[a]Seven eggs from lowest shelf of 28.0°C incubator.
[b]Includes eight eggs from lowest shelf of 28.5°C incubator, which had a mean duration of 59.6 days.
[c]Includes eight eggs from lowest shelf of 28.8°C incubator, which had a mean duration of 56.0 days.
[d]Eight eggs from lowest shelf of 29.5°C incubator.
[e]Eight eggs from lowest shelf of 30.5°C incubator.
[f]Includes 10 eggs transferred from erratic incubator, which had a mean duration of 56.7 days.
[g]Includes 14 eggs transferred from erratic incubator, which had a mean duration of 55.6 days.

28.5°C). Data for the full and restricted sample sets gave similar values (Tables 3 and 5).

The establishment of geographical differences or similarities is complicated by the difference between the two clutches from Florida (Fig. 3). Clutch G produced significantly more males in the incubators at 28.5, 28.8, and 29.5°C (χ^2: $P < 0.02$, two-tailed). Even in the incubator at 30.4°C, an almost entirely feminizing temperature (0% males in all other clutches), Clutch G produced 15% males.

Incubation durations

Table 7 collates information on incubation duration from the three areas sampled. The data are from the field and include the time between hatching and emergence above ground. For the main nesting season, June and July, the data suggest that incubation takes about 8 days longer in Georgia than Florida. However, the Florida incubation times are based on 1 year only (1986). In case the sand temperatures in this year were unusually high, it may be more conservative to compare the Florida data with those for the warmest year in Georgia (1980, shortest incubation times, Table 7). This still leaves a difference of almost 5 days between incubation durations in Georgia

The incubation times in the middle of the season for North Carolina in Table 7 are a further 6 days longer than those for Georgia. The North Carolina data are for 1 year. In case the sand was unusually cool in North Carolina in that year, it may be more conservative to compare the data with those for the coolest year in Georgia (1984, longest incubation times, Table 7). This still leaves at least 2 days difference between North Carolina and Georgia.

Summarizing, the actual data available (Table 7) indicate that incubation times are about 14 days longer in North Carolina than in Florida. More conservatively, this difference might be reduced to about 7 days. However, it is unlikely that both the whole of 1986 was unusually warm in Florida and the whole of 1984 was unusually cool in North Carolina. Therefore, for the purposes of discussion in this paper, an intermediate working figure of 10 days is taken as the approximate difference in incubation duration between the northern and southern loggerhead turtle nesting beaches.

Discussion

The combined pivotal temperature of 29.0°C (Table 3) is below the 30.0°C reported previously for loggerhead turtle

TABLE 5. Percent females produced for specimens only from shelves that held eggs in all 3 years

	28.0 ±0.5°C	28.5 ±0.6°C	28.8 ±0.4°C	29.5 ±0.3°C	30.4 ±0.4°C	Estimated pivotal temp. (°C)
North Carolina	9.5[a] (21)	29.2 (24)	20.8 (24)	66.7[b] (24)		29.1, 29.2
Georgia		66.7 (27)	60.0 (25)	84.0[c] (25)	100.0[a] (25)	Near but <28.5
Florida		26.5 (34)	35.3 (34)	64.9 (37)	92.3[a,c] (39)	29.2
Overall	9.5 (21)	40.0 (85)	38.5 (83)	71.0 (86)	95.3 (64)	28.8, 29.1

NOTE: Sample sizes are given in parentheses.
[a]The same incubator was run at different temperatures for samples in different years.
[b]Includes the twins, both females.
[c]One intersex not counted as female.

TABLE 6. Mean incubation durations (days) for hatchlings only from shelves that held eggs in all 3 years for different incubation temperatures

	28.0 ±0.5°C	28.5 ±0.6°C	28.8 ±0.4°C	29.5 ±0.3°C	30.4 ±0.4°C
North Carolina	61.4[a] (21)	57.0 (24)	54.8 (24)	52.1 (22)	
Georgia		59.2 (26)	57.2 (20)	54.6 (23)	50.8[a] (22)
Florida		58.8 (31)	56.6 (30)	53.3 (32)	50.3[a] (28)
Overall	61.4 (21)	58.4 (81)	56.2 (74)	53.3 (77)	50.5 (50)

NOTE: Sample sizes are given in parentheses.
[a]The same incubator was run at different temperatures for samples in different years.

eggs from Little Cumberland Island, Georgia (Yntema and Mrosovsky 1982). One explanation of this discrepancy is that no correction factor was applied in the previous work. Since those eggs were in a moist substrate (in some cases in shallow water), perhaps evaporative cooling was greater than with the present incubation methods. Less attention was paid in the earlier work to measuring the temperature on different shelves of the incubators.

The present overall estimate of 29.0°C for the pivotal temperature of North American loggerhead turtles is close to the overall value of 28.6°C given by Limpus et al. (1985) for Australian turtles of this species (cf. Table 1). The pivotal temperature of Surinam leatherback turtles (*Dermochelys coriacea*) is about 29.5°C (Rimblot et al. 1985; Rimblot-Baly et al. 1988), of Surinam green turtles about 28.75°C (Mrosovsky et al. 1984), and of Costa Rican green turtles (*Chelonia midas*), estimated from monitoring sand temperatures in the field, about 28.5°C (Morreale et al. 1982). For Mexican olive ridleys, the pivotal temperature is reported to be near 30°C (McCoy et al. 1983; but see Whitmore et al. 1985). Despite the methodological differences between these studies, there is a relatively narrow spread of values. Perhaps the pivotal temperature is a conservative characteristic, with natural selection working mainly through variations in behaviour (cf. Bull et al. 1982a). This is one reason why more investigation of the sex ratios of turtles nesting in thermally different areas is required.

In the present comparison between loggerhead turtles nesting on northern and southern beaches, all of the pivotal temperatures, in whatever way the data are analysed, were close to it could reasonably be argued that there

are no important differences between the populations or clutches tested and that the detection of fine differences is beyond the limits of resolution of the present methods. For instance, the application of a uniform correction factor for evaporative cooling, based on a few measurements, may not be valid; air currents may vary in different parts of the incubators. Ideally the temperature within each egg should be monitored, and monitored continuously.

It is not the author's intention to overinterpret the data, but they do include items of interest other than the finding that pivotal temperatures are all close to 29.0°C. First, the results from Florida samples provide the best evidence to date of interclutch differences (cf. Bull et al. 1982b). The eggs from the two clutches were placed alternately in the available spaces in the incubators, thus controlling for positional thermal variables, the sample sizes were large, and clutch G produced more males at all four temperatures tested (Fig. 3). A difference of 1°C in pivotal temperatures is enough to be ecologically meaningful because sand temperatures at loggerhead turtle rookeries are often close to 29.0°C (Kraemer 1979).

Second, given the care taken to standardize methodology, it is safe to say that some of the turtles nesting in North Carolina lay eggs with higher pivotal temperatures than some of those from further south in Georgia and Florida; the lower pivotal temperatures for the two clutches from Georgia are not easily dismissed as some minor calibration error that year because even at a given incubation duration these clutches produced relatively more females (Fig. 4). Since it is cooler (longer incubation times) in North Carolina, it is likely that relatively more males are produced on these northern beaches. How
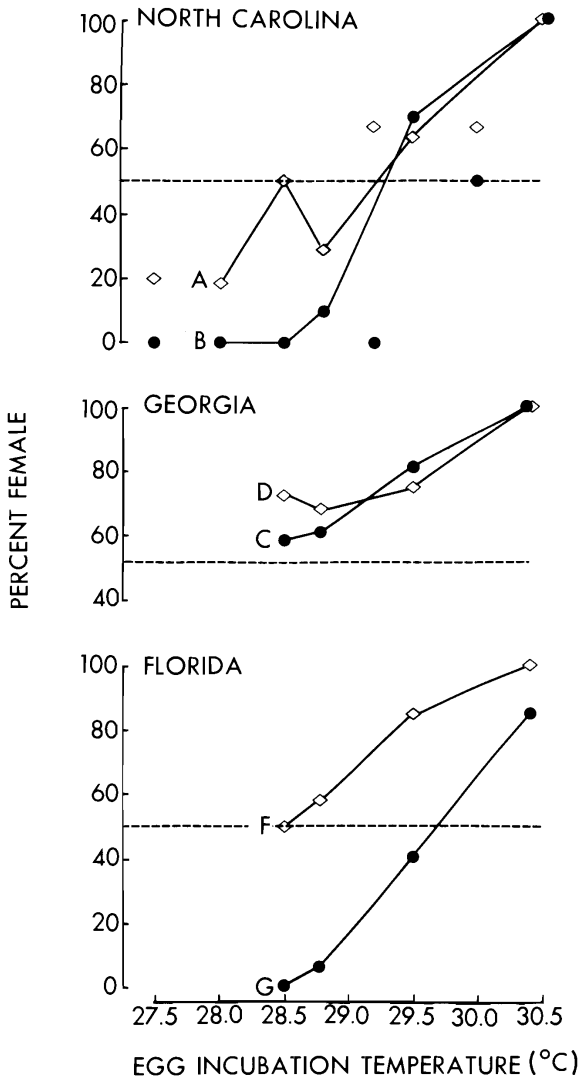
FIG. 3. Sex ratios of six clutches of loggerhead turtle eggs incubated at different constant temperatures. Letters labelling the clutches correspond with those in Table 2. Composition of the groups at different temperatures is the same as in Table 3. Within each area, different symbols represent different clutches. Symbols not joined by lines are based on samples of fewer than seven eggs. Symbols joined by lines are based on samples of more than nine eggs. The horizontal broken line is placed at the 50% female level.

many more depends on the proportion of clutches with different pivotal temperatures in the different areas and this cannot be answered without further sampling. Also the possibility that there are population differences in sensitivity to thermal excursions above and below the pivotal temperature needs to be investigated (see also Bull and Vogt 1981). Nevertheless, a sample of two clutches from each area is better than no sample, and suggests a male bias on the North Carolina beaches.

The likelihood of a male bias in North Carolina is supported by more detailed consideration of the difference of approximately 10 days in incubation duration between North Carolina and Florida. A rule of thumb is that a 1°C difference alters incubation duration by 5 days (Mrosovsky and Yntema 1980).

TABLE 7. Incubation durations (days) of loggerhead turtle eggs for different beaches, years, and conditions

	May 1–16 $\bar{x}(n)$	May 17–31 $\bar{x}(n)$	May 17–31 Range	June 1–15 $\bar{x}(n)$	June 1–15 Range	June 16–30 $\bar{x}(n)$	June 16–30 Range	July 1–16 $\bar{x}(n)$	July 1–16 Range	July 17–31 $\bar{x}(n)$	July 17–31 Range	August 1–16 $\bar{x}(n)$	August 1–16 Range	August 17–31 $\bar{x}(n)$	August 17–31 Range
North Carolina															
Bald Head (1984)[a]		69.0(1)		68.7(17)	61–77	68.3(28)	60–74	65.5(18)	61–69	68.7(11)	62–82	72.7(3)	70–75		
Camp Lejeune (1984)[a]		69.0		72.3(9)	65–80	68.6(15)	61–76	69.4(9)	60–76	72.8(13)	66–83	83.0(2)	80–86		
Mean duration				70.5		68.5		67.5		70.8		77.9			
Georgia															
Little Cumberland Island[b]															
1980		60.3(4)	56–64	60.4(12)	56–66	58.4(11)	53–62	56.8(10)	52–60	59.5(8)	57–62	72(1)			
1982	73.0(1)	69.0(5)	66–72	66.2(13)	58–69	64.7(12)	62–68	65.3(17)	63–68	67.2(5)	65–71				
1983		70.4(7)	67–74	64.1(13)	61–68	59.4(13)	55–63	58.5(15)	57–60	61.5(15)	58–71				
1984		76.7(3)	72–82	68.0(10)	66–72	64.4(13)	59–68	66.5(11)	62–71	68.8(5)	65–71				
1985		64.1(9)	60–71	64.1(13)	60–68	62.8(12)	57–67	60.1(11)	58–62	64.8(5)	62–67	77.5(2)	68–87		
Mean duration	73.0	68.1		64.6		62.0		61.4		64.4		74.8			
Florida															
Hobe Sound															
1986[b]	61.0(1)	58.3(3)	55–60	57.0(6)	56–58	53.0(2)	52–54	53.0(3)	53–53	53.0(5)	51–56	51.6(9)	49–54	48.0(2)	48–48
1986[c]		59.2(13)	56–64	57.9(16)	55–60	54.2(22)	50–57	53.1(19)	51–55	52.8(19)	49–55	51.7(3)	50–53	52.0(1)	
Mean duration	61.0	58.8		57.5		53.6		53.1		52.9		51.7		50.0	

NOTE: Dates given are laying dates. Mean values of the means for each laying period for each region are given. Sample sizes are given in parentheses.
[a] Mixture of reburied and undisturbed nests.
[b] From clutches reburied on the beach in centrally located hatcheries.
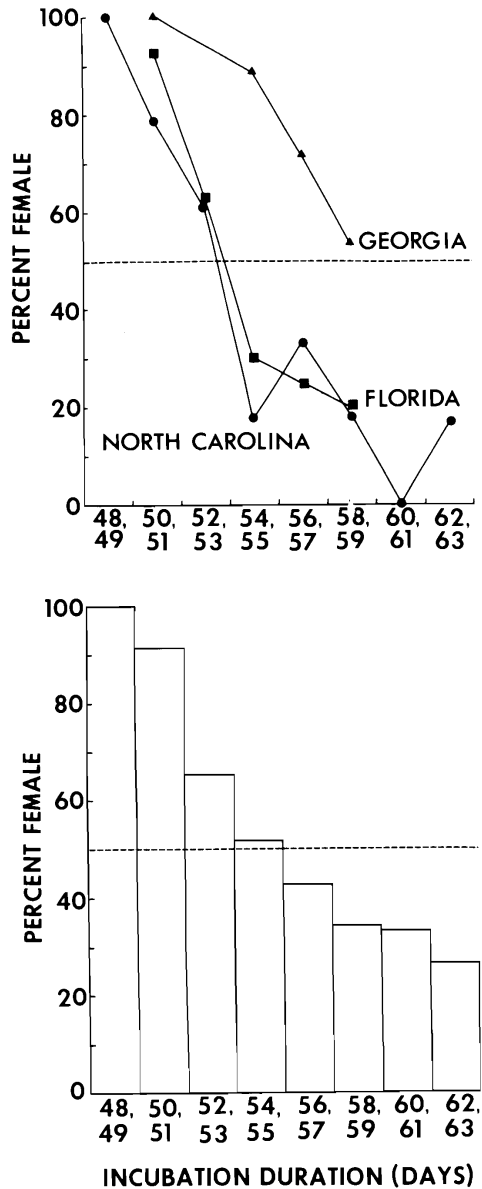[c] From nests left in situ.

FIG. 4. Sex ratio as a function of incubation duration. The histogram is based on the combined data from all six clutches (bars are based on *n* values of 15 or more). The top part of the figure shows the data separately for the three areas (points based on *n* values of < 10 have been omitted). A horizontal broken line is drawn at the 50% female level; the intersection of this line with the sex ratio gives the pivotal incubation duration.

Therefore 10 days represents about 2°C difference in incubation temperature, enough to have important effects on sex ratio given the steepness of the changes of sex ratio with temperature (Fig. 3). Moreover, when the data on sex ratio obtained in the laboratory are plotted as a function of incubation duration (Fig. 4), it can be seen that a difference in duration of 10 days makes a 35−65% difference in sex ratio, depending on which part of the curve the 10 days span. It might eventually be possible to use such curves to estimate sex ratios of hatchlings in the field from data on their incubation durations, but first it

would be necessary to obtain additional information on a variety of related points.

Incubation durations in the field include the time it takes after hatching for a neonate turtle to make its way to the surface. This time would have to be subtracted from field incubation durations before they could be compared to a standard laboratory curve.

Unfortunately few studies of hatching to emergence time have been made and some of these were not in natural nests. Carr and Ogren (1960) observed that a clutch of green turtles in a glass-sided container took 7 days to reach the surface after hatching. Green turtle nests are deeper than those of loggerhead turtles. Raj (1976) placed a microphone in an artificial hawksbill nest. Sounds were recorded as early as 6 days before emergence. But it is not possible to tell whether the first sounds came from hatching itself or from movement within the eggs. Neonates from two hawksbill clutches took 4−6 days to leave artificial glass-sided nests (Diamond 1976). Kraemer and Richardson (1979) recorded changes in the heights of discs resting on the top of the egg mass for more than fifty loggerhead clutches. From slight changes in the rate of change of the height of the discs, they inferred that hatching occurred about 4−6 days before emergence and that digging up to the surface took no more than 3 days after that. However, a straight line can be placed through their data and still be within the 95% confidence limits of most of their points; this makes it harder to detect discontinuities in the position of the disc at hatching. Given the rather unsatisfactory data on this topic, a round figure of 5 days might serve as a provisional figure for hatching to emergence time for loggerhead turtles. However, the possibility that emergence time may vary seasonally should be kept in mind. If warmth inhibits the activity of hatchlings within the nest, as it does once they have emerged (Mrosovsky 1968), then heat-induced lethargy in the summer may slow the progress of hatchlings toward the surface. Compaction of the sand may also vary with the amount of rainfall. The influence of such seasonal variables on emergence time remains to be determined.

To use incubation times to estimate sex ratios, consideration must also be given to the fact that temperatures in nature are not as constant as those in the laboratory. It is the temperature during the middle third of incubation that determines the direction of sexual differentiation (Yntema and Mrosovsky 1982). If temperature during this critical period correlated well with the total incubation duration, it might still be possible to estimate the approximate sex ratio produced by a population of turtles. Any such method would be enormously helpful in demographic work because, in contrast to the laboriousness and other drawbacks of histological work on sex ratio, large data sets on incubation duration are easily obtained.

In addition, major demographic questions remain to be answered. If hatchlings from northern loggerhead turtle beaches are mostly males, how is the population maintained there? In fact rather few turtles nest in North Carolina (Crouse 1984). Perhaps this is because few females are produced. Another possibility is that females may come to these beaches, although they themselves were born elsewhere. Nest-site specificity in some loggerhead turtles may not be especially strong. Nesting by the same animal on both the Gulf coast and the Atlantic coast of Florida has been recorded (Le Buff 1974). To the extent that sea turtle populations are not divided into reproductively isolated subgroups with their own rookeries, conserving all major beaches on a long stretch of coast may

become less important. To the extent that thermally different parts of the coast contribute males and females differentially to a larger interbreeding population, conserving different regions may be necessary for maintenance of natural sex ratios.

Acknowledgements

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